

ABSTRACT.--A great amount of plant photosynthate is released from roots and supports a large and diverse population of soil organisms which greatly influence root growth and forest regeneration. This myriad of soil organisms and their interactions affect capture and uptake of plant nutrients and water, and contribute to the development and stability of soil structure. Numerous natural and man-caused activities can disturb above- and below-ground environments and potentially impact beneficial soil organisms and subsequent regeneration. Activities that minimize losses of organic matter, topsoil and soil porosity have the least impact. Diminished root and mycorrhiza formation on seedlings outplanted onto disturbed sites can slow regeneration, especially in areas where the period favorable for seedling growth is short. Ectomycorrhizal fungi supported by non-coniferous hosts can actively colonize feeder roots of conifer seedlings. Thus, seedlings may "plug into" the network of compatible ectomycorrhizal hyphae supported by pioneering hardwood species, thereby gaining opportunity for early ectomycorrhizal formation and establishment on harsh sites. Management strategies that avoid negative impacts on the belowground ecosystem are discussed and encouraged.

SOIL ORGANISM-ROOT INTERACTIONS

Plants allocate a high proportion of photosynthate to roots. In forest trees, a surprisingly large amount is diverted to roots and mycorrhizae (the combination of fungus and root tissue) or exuded into the immediately surrounding area - rhizosphere or mycorrhizosphere. In Pacific silver fir (*Abies amabilis*) ecosystems (Vogt *et al.* 1982) 70% to 80% of net primary production occurs in

roots and ectomycorrhizae. Similar values have been reported in Douglas-fir ecosystems (Fogel and Hunt, 1983). The great amount of photosynthate flowing from roots, ectomycorrhizae and ectomycorrhizal fungus hyphae support a large, diverse community of soil organisms. This is not energy lost to the plant. This myriad of soil organisms and their interactions greatly influence forest regeneration and root growth through a variety of direct and indirect processes. This includes protecting roots from some soil pathogens, maintenance of soil structure, fixation of nitrogen, capture and uptake of nutrients and ameliorating plant moisture stress.

Mycorrhizal fungi are perhaps the best known rhizosphere organisms. Roughly 90% of all plant species form some type of mycorrhiza. There are two broad groups of mycorrhizal fungi: those forming "ectomycorrhizae", so termed because there is an obvious external modification of root morphology and color, and "vesicular-arbuscular mycorrhizae"-- the name coming from structures produced within plant cells and resulting in no external modification of the root. Ectomycorrhizal fungi associate with most

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² M.P. Amaranthus and R. Molina, United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR, U.S.A. 97331 and D.A. Perry, Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR, U.S.A. 97331

of the important commercial forest tree species of temperate and boreal zones and 70% of species planted in the tropics. Ectomycorrhizae improve seedling survival by enhancing uptake of water and nutrients (especially phosphorous), lengthening root life and protecting against pathogens.

Ectomycorrhizae form the first layer surrounding feeder roots and influence the character of exudates and microbial species composition in surrounding soil (Meyer and Linderman 1986). For example, ectomycorrhizal plants can have fewer pathogens and perhaps more nitrogen-fixing bacteria in their rhizospheres than nonmycorrhizal plants (M.P. Amaranthus, C.Y. Li, and D.A. Perry, in press). Many other soil organisms influence plant growth. Roots and mycorrhizal hyphae extending through soil exude amino acids, carbohydrates and other organic compounds that stimulate growth of soil microorganisms such as bacteria and actinomycetes. These microorganisms in turn produce their own compounds that can either stimulate or repel other soil organisms. Bacteria and actinomycetes are prime food sources for "grazer" organisms such as mites, nematodes, amoebae, and springtails. These grazers then fall prey to carnivores such as centipedes and spiders. Saprophytic organisms feed on dead remains of other organisms accumulating in the rhizosphere, mineralizing complex organic molecules to plant-available forms. Nutrients released through decomposition are captured and transported back to forest plants via a network of mycorrhizal fungus hyphae, thus completing the cycle.

Soil structure can influence forest regeneration and root growth. Ectomycorrhizal fungi and other soil organisms affect soil structure by producing humic compounds, accelerating decomposition of primary minerals, and secreting organic "glues" (extracellular polysaccharides) that bind soil particles into water-stable aggregates (Perry *et al.* 1987). Aggregate stability is essential for development and maintenance of pores that allow movement of water and air to soil organisms and roots. Continued aggregate stability depends upon flow of organic glues for linking mineral grains and homogeneous clays. Interrupting flow of organic materials can affect soil structure (J.G. Borchers and D.A. Perry, in press).

Inadequate nitrogen is the most common limitation to forest growth in the Douglas-fir region. Loss of nitrogen due to timber harvest, residue removal, and site preparation (especially intense burning) often exceeds natural inputs to the forest over the length of most planned rotations (Perry and Rose, 1987). Biological fixation of atmospheric nitrogen by soil organisms may be the most practical and economical means of replacing losses related to disturbance. (Gordon and Avery, 1985).

Symbiotic nitrogen fixation in root nodules can add substantial amounts of nitrogen to Pacific Northwest forests (Wollum and Youngberg 1964). Root nodule plants such as lupine, alder, and snowbrush (*Lupinus*, *Alnus*, and *Ceanothus* species) form a mutually beneficial relationship with certain bacteria and actinomycetes that convert atmospheric

nitrogen into ammonium. Asymbiotic, "free-living" microorganisms also contribute to the nitrogen pool. Nitrogen-fixing bacteria have been found in association with wood-rooting fungi in forest residues (Larsen *et al.* 1980). *Azotobacter*, *Clostridium*, and *Azospirillum* bacterial species fix nitrogen in the rhizosphere and mycorrhizosphere where oxygen levels are low (M.P. Amaranthus, C.Y. Li, and D.A. Perry, in press). Nitrogen availability strongly influences health and vigor of individual seedlings and thus their ability to become established.

SOIL ORGANISMS AND FOREST DISTURBANCE

Soil organisms are not distributed homogeneously within soil but rather in islands of intense activity centered around energy (carbon) sources such as roots, mycorrhizae and mycorrhizal hyphae. What happens to populations of soil organisms following forest disturbance when energy inputs from plants are reduced or eliminated? Populations of organisms depending upon those plants, such as mycorrhizal fungi and other rhizosphere organisms, die, form resting bodies or are replaced. If the energy source is not restored, populations of organisms are likely to shift to a higher proportion of saprophytic organisms than before. Composition of the bacterial community changes in soil not influenced by living plant roots. Bacteria in rhizospheres have very different nutritional requirements than those in open soils. For example, populations of nitrogen-fixing *Rhizobium* species decline quickly in absence of hosts (Corman *et al.* 1987).

The ability of forest soils to maintain viable populations of mycorrhizal fungi, particularly after disturbance, is referred to as the mycorrhizal inoculum potential. Several environmental, biological, and soil physical factors affect the inoculum potential and thus our ability to predict impacts following disturbance. Persistence of mycorrhizal fungus spores and hyphal fragments varies with climate and soils. For example, ectomycorrhizal fungus spores and hyphal fragments remained metabolically active after two years in Scandinavian forests, though the number of active fragments dropped dramatically over that period (Ferrier and Alexander 1985). The active period may be predictably shorter in warmer climates to the extent that fragment survival is related to respiration rates.

Ectomycorrhizal fungi that fruit above ground (mushrooms) produce wind disseminated spores that may enter disturbed sites at high rates when conditions for fruiting are optimal. Many ectomycorrhizal fungi fruit beneath the soil surface (truffles) and mammals that consume them are primary vectors for dissemination. Conditions that affect animal movements from disturbed to undisturbed areas, such as vegetation and logs, could affect spore input. Past work strongly suggests, however, that survival of propagules and input of spores are insufficient to maintain mycorrhizal potential of

disturbed sites in absence of living hosts (Perry et al. 1987, Amaranthus and Perry 1987). In the Pacific Northwest, ectomycorrhiza formation on seedlings generally decreases as length of time between disturbance and reforestation increases (Pilz and Perry 1984, Parke et al. 1984, Amaranthus and Perry 1987).

Numerous natural and man-caused activities can disturb above- and below-ground environment and therefore potentially impact populations of soil organisms and forest regeneration. Because organic matter is a center of soil microbial activity, degree of organic matter lost from a site can influence populations of organisms, such as mycorrhizal fungi (Amaranthus et al. 1989, Harvey et al. 1979). Harvey et al. (1979) found more than 87% of active ectomycorrhizae in a mature Douglas-fir/larch (*Larix*) forest occurred in humus and decaying wood. Moreover, physical consumption of humidified material affects not only ectomycorrhizae but an array of soil organisms tied to forest regeneration. Habitat can also be lost for small mammals that distribute fungal spores of several mycorrhizal fungi (Maser et al. 1978). The number, diversity and activity of beneficial soil organisms can be reduced by repeated removal of organic matter from a site.

A variety of organic matter types may be critical to support root and mycorrhizal activity. Harvey et al. (1986) found that during periods of adequate soil moisture, humus supported highest levels of ectomycorrhizae, but during periods of drought buried wood becomes the most active site. Importance of decaying wood to support root and mycorrhizal activity may be most important following disturbance such as wildfire. In southern Oregon and northern California, decaying wood contains 25 times more moisture following drought and intense fire compared to soil and is a center of root and mycorrhizal activity for pioneering forest vegetation (Amaranthus et al. 1989).

By minimizing soil compaction and preserving soil structure we can maintain populations of beneficial soil organisms and ensure adequate root growth. Pore space is essential for movement of oxygen and water into soil and flushing out of carbon dioxide. Activity of roots, mycorrhizae and soil organisms is drastically altered when levels of these basic elements become extreme. Undisturbed forest soil is rarely saturated because large pores allow for rapid downward percolation of water. However, when soils are compacted, large pores are destroyed and water movement is reduced. Soil compaction greatly influences types and activities of soil organisms sensitive to excess moisture. Adverse response of forest regeneration reflects indirect effect on soil organisms and direct effects on roots themselves. Careful selection and skillful implementation of harvest methods to minimize compaction maintains beneficial soil organisms, root growth and forest regeneration.

Topsoil is a reservoir of nutrients as well as fungal spores and other propagules important for mycorrhiza formation and root growth. Loss of this biological reservoir by erosion will impair natural

and managed forest regeneration. Reeves et al. (1979) found that all dominant species in a sagebrush (*Artemisia*) community in Colorado were mycorrhizal. When topsoil was disturbed and eroded, the numbers of mycorrhizal fungus propagules were greatly reduced (Moormand and Reeves 1979), and nonmycorrhizal weedy species quickly established and dominated the site. Little is known about the effects of soil erosion from deforested areas, but the density and diversity of mycorrhizal fungus inocula can be reduced.

RAPID ROOT TIP AND MYCORRHIZA FORMATION, AND FOREST REGENERATION

Successful forest regeneration depends upon the capacity of tree seedlings to quickly capture site resources. Early root tip and mycorrhiza formation provide rapid nutrient uptake and the subsequent vigor seedlings need to resist pests, pathogens and survive climatic stress.

The importance of early mycorrhiza formation for seedlings to successfully establish in dry areas has been emphasized (Trappe 1977, Perry et al. 1987, 1989). Dry climates may limit activity of mycorrhizal fungi by decreasing the time for spore production, germination and mycelial growth in the soil. Ectomycorrhizal fungi also differ in their capacity to function in periods of either low or excessive soil moisture and impaired function will subsequently affect seedling growth and successful forest regeneration (Parke et al. 1987).

Cold climates can also effect root tip production, ectomycorrhiza formation and subsequent forest regeneration. Seedlings growing in cold climates require rapid root tip and ectomycorrhiza formation to take advantage of the short growing season and obtain necessary nutrients and water to survive the long cold season and early frosts. On stressful sites, the period favorable for root growth may be brief. In the Klamath Mountains of northwest California and southwest Oregon, Amaranthus and Perry (1987, 1989a, 1989b) found that root tip and ectomycorrhiza formation strongly influences seedling survival and growth on sites limited by moisture and temperature. Under such limiting conditions, factors that enhance rapidity of root tip and ectomycorrhiza formation produce vigorous seedlings. Thus, selecting management practices that do not further exacerbate potentially stressful sites by damaging the belowground ecosystem will be instrumental in developing a successful integrated scheme for reforestation.

The maintenance of certain brush species following site disturbance may be important in ameliorating the harsh conditions for seedling establishment. In southwest Oregon and northern California, species in the families Ericaceae, Fagaceae, Pinaceae, Pyrolaceae, Rosaceae, and Betulaceae form ectomycorrhizae and associate in common with many fungal species (Molina and Trappe 1982). Ericaceous manzanitas (*Arctostaphylos* spp.) and Pacific madrone (*Arbutus menziesii* Pursh) are

early pioneers after timber harvest and fire. Ectomycorrhizal fungi supported by nonconiferous hosts, such as manzanita and madrone, can actively colonize feeder roots of conifer seedlings. Thus, seedlings may "plug into" the network of compatible ectomycorrhizal fungus hyphae supported by surrounding ericoids, thereby gaining opportunity for early ectomycorrhiza formation critical for establishment on harsh sites (Amaranthus *et al.* 1989).

Choquette, Schroeder, and Perry (unpublished) examined the effects of madrone on conifer regeneration on 76 circular 3m plots on a steep south-facing harvest unit in the southern Oregon Cascades. They found nearly 5X more young conifer trees under madrone compared to all other brush species or in the open (Table 1).

TABLE 1.--Numbers of young conifer trees (<2.5m tall) under Pacific madrone vs. all other brush species or in the open.

	Under madrone	All species or in open
# of conifers per ha	5486 ^a	1192
standard error	1821	208

^aSignificantly different at $p \leq 0.05$

In 1986, Amaranthus (unpublished) examined the effect of greenleaf manzanita (*Arctostaphylos patula*) on number and rapidity of Douglas-fir root tip and ectomycorrhiza formation in southern Oregon. The study site was in a 20 year-old nonreforested clearcut that had been invaded largely by nonectomycorrhizal annual plants and scattered clumps of ectomycorrhizal manzanita. Nonmycorrhizal 1-0 containerized Douglas-fir seedlings were planted at 0.3, 1.2 and 3.6 meter distances from manzanita clumps and sampled on three dates during the growing season. Douglas-fir seedlings nearest manzanita formed significantly greater number of root tips early in the growing season (Table 2A). Douglas-fir ectomycorrhiza formation was also greatest nearest manzanita (Table 2B). Number of manzanita mycorrhizal tips from core samples were significantly higher closest to manzanita (Table 3). Soil moisture did not differ significantly with distance from manzanita for the three sample dates.

Differences in light, temperature and moisture beneath hardwoods could influence abundance of conifer regeneration, root, and ectomycorrhiza formation. D. Minore (personal communication) investigated the physical environment beneath sprouting hardwood clumps in 8 clearcuts in southwest Oregon. Soil moisture was higher and soil temperature was lower beneath clumps than in the open. Light intensity was higher beneath madrone compared to tanoak and chinkapin. Soil organisms also influence close association of conifers with some pioneering hardwoods (Amaranthus *et al.* 1989). Root-chamber analysis of development of ectomycorrhizal mycelium has shown that expanding

hyphal fans not only act as nutrient-absorbing structures but also colonize nonmycorrhizal feeder roots in host-plant combinations within and among species. Using radioactive labeling, Finlay and Read (1986) have demonstrated free movement of carbon among plants connected by mycorrhizal mycelium. Clearly existence of "pipelines" for distributing materials among plant species has important implications for forest regeneration.

In summary, healthy populations of mycorrhizal fungi and other soil microbes are essential for the growth and survival of tree seedlings, particularly on droughty or nutrient-poor sites. Protecting the below-ground ecosystem is an important component of successful reforestation. In the conifer forests of southern Oregon and northern California, numerous early successional hardwood trees and shrubs stabilize soil organisms that are beneficial to conifers following wildfire or clearcutting. Vegetation management should aim at retaining some of these noncrop species for long-term soil protection.

Table 2.--Average number of Douglas-fir root tips (A) and ectomycorrhizal tips (B) per seedling at 0.3, 1.2 and 3.6 meter distances from manzanita clumps on three sample dates in an old, nonreforested clearcut in southwest Oregon.¹

(A) Sample date 1986	Distance from manzanita (m)		
	0.3	1.2	3.6
May 25	119a	86b	70b
June 15	108a	94ab	68b
July 15	98a	105a	102a
(B)			
May 25	0a	0a	0a
June 15	13a	0b	0b
July 15	15a	4b	4b

¹Row numbers sharing same alpha character not significantly different at $p \leq 0.05$

Table 3.--Average number of manzanita mycorrhizal tips per 300 cc soil at 20cm depth at 0.3, 1.2 and 3.6 meter distances from manzanita clumps on three sample dates in an old nonreforested clearcut in southwest Oregon.¹

Sample date 1986	Distance from manzanita (m)		
	0.3	1.2	3.6
May 25	17a	3b	0b
June 15	19a	6b	0c
July 15	48a	0b	0c

¹Row numbers sharing same alpha character not significantly different at $p \leq 0.05$

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